

The Fish Fauna of Lake Victoria during a Century of Human Induced Perturbations

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ABSTRACT

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Lake Victoria, by area the largest tropical lake of the world, is well-known for its diverse native fish fauna, which comprised about 500 endemic haplochromine cichlid species, two tilapiine species and 46 other species belonging to 12 families. During the past decades, the fish species diversity in the lake has declined dramatically due to human induced perturbations in the ecosystem. Based on literature and our own research findings we provide an overview of these changes and their most likely causes. During the first half of the last century, the increasing fishing pressure had a great impact on the native tilapiine cichlids and other large fish species. The shift in fish landings showed a classic example of fishing down the food web. Because of the dwindling catches, the Nile perch and four exotic tilapiine cichlids were introduced into the lake in the 1950s. Dramatic changes in the fish fauna occurred in the 1980s, with the upsurge of the introduced Nile perch and Nile tilapia, the decline of wetland zones, and increased eutrophication of the lake. The native tilapiines were replaced by the Nile tilapia, and several of the catfish species showed a dramatic decline, as did the lungfish. Most severely hit were the haplochromine cichlids, which disappeared from large parts of the lake, probably resulting in the extinction of many species. The introduced Nile perch and Nile tilapia, and the native cyprinid *Rastrineobola argentea* became the dominant fish species. Though water quality deteriorated and fish diversity decreased, fish landings rose from about 100,000 t y⁻¹ in the 1970s to approximately 1 million t y⁻¹ in the period 2005-2007. Since 1999 the biomass of Nile perch declined, whereas that of *R. argentea* increased. In the same period some of the sublittoral haplochromine species have recovered. Some of the surviving fish species, show remarkable changes in ecological and morphological features relative to the pre-Nile perch period, which seem to be adaptive responses to the changed environment. Although it may be possible to reconcile fisheries sustainability with biodiversity conservation in the lake basin, measures to reduce environmental stress in the lake are an urgent issue.

Keywords: biodiversity, environmental degradation, eutrophication, extinction, fishery, haplochromine cichlids, Nile perch, speciation, species introductions

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INTRODUCTION

With a surface area of 68,800 km², Lake Victoria is the largest tropical lake in the world. It has a maximum depth of 70 m, which is relatively shallow compared to other large lakes in East Africa (Fryer & Iles 1972). The lake is well known for its high fish species diversity, dominated by haplochromine cichlids (Greenwood 1974; Seehausen 1996; Witte *et al.* 2007a). During the past century, dramatic anthropogenic changes were observed in the lake's ecosystem. Fishery, species introductions and increasing eutrophication had an enormous impact on the fish fauna of the lake (e.g. Ogutu-Ohwayo 1990a; Witte *et al.* 1992; Verschuren *et al.* 2002; Hecky *et al.* 2010). The present paper aims to give a review of the changes in the fish fauna of Lake Victoria and to discuss the potential causes of these changes. For this purpose we roughly divided the history of the lake over the past century into two periods: (1) before and during the 1980s and (2) after the 1980s.

LAKE VICTORIA AND ITS FISH DIVERSITY BEFORE AND DURING THE 1980S

More than 500 endemic haplochromine cichlid species, all maternal mouth brooders, are known from Lake Victoria (Greenwood 1974; Kaufman & Ochumba 1993; Seehausen 1996; Witte *et al.* 2007a). Furthermore, Lake Victoria used to harbour two native tilapiine cichlids, and 46 native non-cichlid species (Table 1), of which 16 are endemic to the lake and its drainage basin (Greenwood 1974; van Oijen 1995). The native non-cichlid species belong to 12 families (Table 1; Fig. 1). In the 1950s, the Nile perch, *Lates niloticus* (Linnaeus, 1758), Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758) and three other tilapiine species were introduced into the lake (Welcomme 1988; Pringle 2005).

From the end of the 1960s till the beginning of the 1980s, the haplochromine cichlids made up more than 80% of the demersal fish catches (Fig. 2b; Kudhongania & Cordone 1974). Other prominent species in bottom trawl catches were *Oreochromis esculentus* (Graham, 1929), *O. variabilis* (Boulenger, 1906), *Clarias gariepinus* (Burchell, 1822), *Protopterus aethiopicus* Heckel, 1851 and *Bagrus docmak* Forsskål, 1775 (Kudhongania & Cordone 1974; Goudswaard & Witte 1997; Goudswaard *et al.* 2002a, b). Apart from these demersal fishes, the small pelagic cyprin-

Table 1. Total number of fish species native to Lake Victoria arranged by family and number of species that were introduced into the lake. Sources: Greenwood 1966, 1974; Kaufman & Ochumba 1993; van Oijen 1995; Seehausen 1996; Witte *et al.* 2007a.

Families/tribes	Number of native species	Introduced species
Protopteridae	1	
Mormyridae	7	
Alestidae	2	
Cyprinidae	17	
Bagridae	1	
Schilbeidae	1	
Clariidae	6	
Mochokidae	2	
Nothobranchiidae	2	
Poeciliidae	5	
Latidae		1
Cichlidae/ haplochromines	ca 500	
Cichlidae/ tilapiines	2	4
Anabantidae	1	
Mastacembelidae	1	

nid *Rastrineobola argentea* (Pellegrin, 1904) made an important contribution to the fish fauna in the lake (Okedi 1974).

Lake Victoria haplochromines have been classified into 15 (sub)trophic groups, each consisting of species sharing morphological characters related to the capture, uptake, and processing of their dominant food source (Greenwood 1974; Witte & van Oijen 1990). The distribution of trophic groups is habitat dependent. For instance, epilithic algae grazers are restricted to rocky shores; insectivores and oral shelling molluscivores are mainly associated with hard substrates like sand and rocks; and detritivores are concentrated near mud bottoms (e.g. Greenwood 1974; Witte 1981; Witte *et al.* 1992; Seehausen *et al.* 1997b).

With respect to the total number of species, the piscivores and insectivores were the most common groups (Fig. 3a), however, the detritivores and zooplanktivores were the most important with respect to biomass, at least in the sub-littoral habitat (6-20 m deep; Fig. 3b), and probably also in the open waters of the lake.

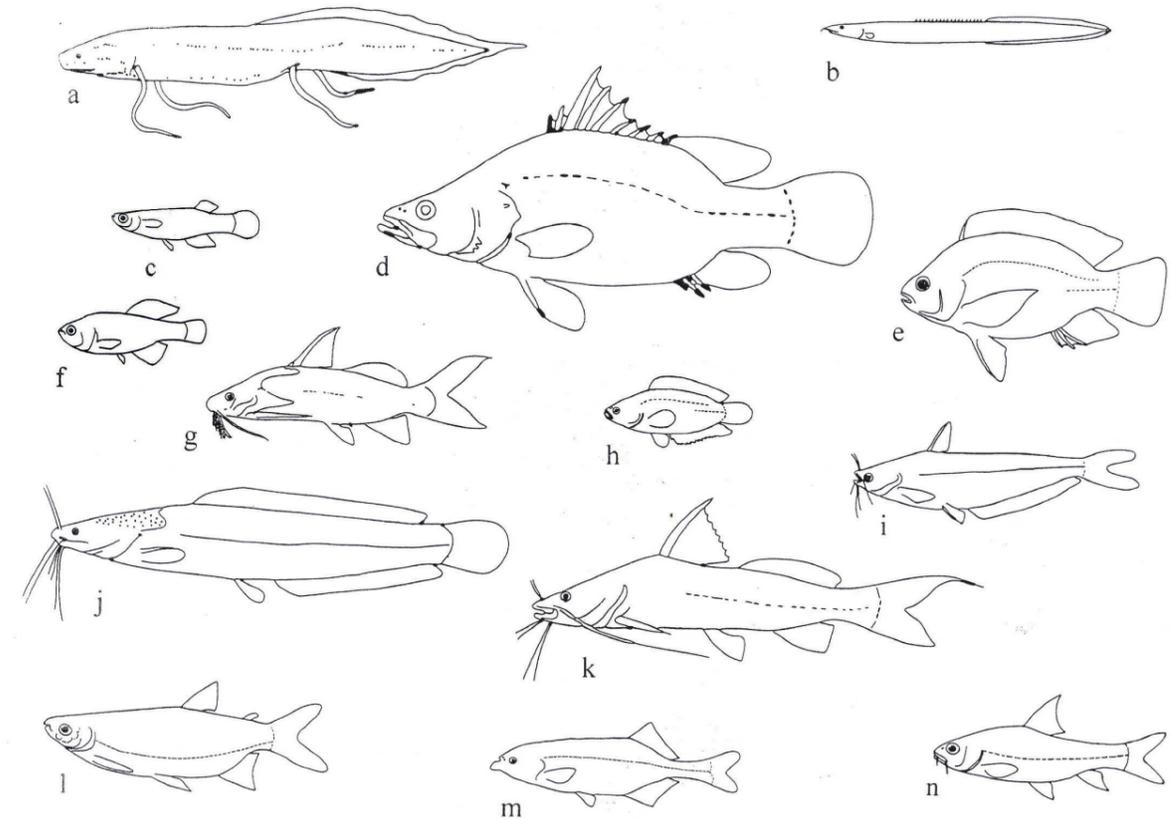


Fig. 1. Outline figures of representatives of the fish families in Lake Victoria. a, Protopteridae; b, Mastacembelidae; c, Poeciliidae; d, Latidae; e, Cichlidae; f, Nothobranchiidae; g, Mochokidae; h, Anabantidae; i, Schilbeidae; j, Clariidae; k, Bagridae; l, Alestidae; m, Mormyridae; n, Cyprinidae (after van Oijen 1995).

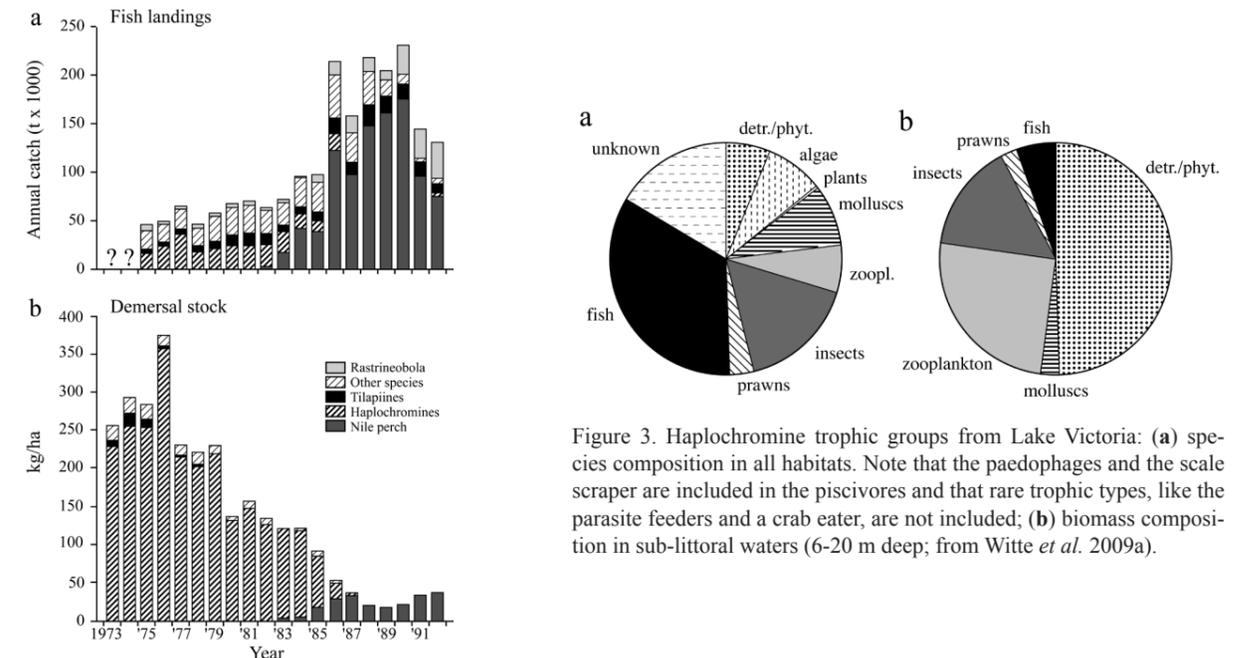


Fig. 2. Changes during the 1970s and 1980s in (a) total fish landings in the Tanzanian part of Lake Victoria and (b) demersal fish stocks in the Mwanza Gulf (Tanzania) calculated from bottom trawls catches. The decline of haplochromines in the bottom trawl catches in the Mwanza Gulf in the period 1973-1984 was mainly due to trawl fishery; the subsequent further decline was caused by the Nile perch upsurge. Note that bottom trawls did not catch the small pelagic *Rastrineobola argentea*. After 1985, Nile tilapia dominated the tilapiine catches (after Witte *et al.* 1999).

Figure 3. Haplochromine trophic groups from Lake Victoria: (a) species composition in all habitats. Note that the paedophages and the scale scraper are included in the piscivores and that rare trophic types, like the parasite feeders and a crab eater, are not included; (b) biomass composition in sub-littoral waters (6-20 m deep; from Witte *et al.* 2009a).

Several authors have raised doubts about the taxonomic status of Lake Victoria haplochromines (e.g. Sage & Selander 1975; Meyer 1987). However, ecological research corroborated in many cases the biological soundness of species distinction originally based on male colouration and small morphological differences; viz. no indications of gene flow could be found between presumed species that live in sympatry (Hoogerhoud *et al.* 1983; Goldschmidt & Witte 1990; Seehausen *et al.* 1998, 2008).

Molecular studies suggest that the 500+ haplochromine species of Lake Victoria evolved within the geologically short period of 100,000–400,000 years (Meyer *et al.* 1990; Nagl *et al.* 2000; Seehausen *et al.* 2003; Verheyen *et al.* 2003). However, paleolimnological data indicate that Lake Victoria was completely dry between 18,000 and 15,000 years ago (Johnson *et al.* 1996; Stager & Johnson 2008). The discrepancy between these data resulted in vigorous debates about the origin, age, and evolutionary history of the extraordinary speciose Lake Victoria haplochromines (e.g. Nagl *et al.* 2000; Seehausen *et al.* 2003; Verheyen *et al.* 2003; Fryer 2004; Seehausen 2006; Elmer *et al.* 2009). Nagl *et al.* (2000) suggested that the Lake Victoria haplochromines originated from trophic generalists, which lived in the East-African river systems and in which mutations for morphological adaptations were already present as polymorphisms. Data of Seehausen *et al.* (2003) indicated that the Lake Victoria–Edward flock is derived from the morphologically and ecologically diverse cichlid genus *Thoracochromis* from the Congo and Nile. Verheyen *et al.* (2003) explained the fast radiation of eco-morphological diversity in Lake Victoria haplochromines by their descent from the lacustrine, possibly already diversified, Lake Kivu ancestors, a view confirmed by Elmer *et al.* (2009). All these papers suggest that the Lake Victoria cichlid flock *sensu stricto* must be older than 15,000 years, and is not strictly monophyletic. Elmer *et al.* (2009) estimated that the most recent common ancestor of the cichlids of lakes Victoria, Albert, Edward, George, Kivu and Kyoga together (the Lake Victoria region ‘super flock’) existed about 4.5 million years ago. They also suggest that the Pleistocene desiccation ‘bottlenecked but did not extirpate’ the adaptive radiation of Lake Victoria haplochromines.

Rapid speciation has been suggested to be a typical feature of haplochromine cichlids (Seehausen 2006) and is thought to be mainly the result of sympatric

speciation through disruptive sexual selection for conspicuous coloration (Maan *et al.* 2004; Seehausen *et al.* 2008) and strong assortative mating (Seehausen & van Alphen 1998). Learning in the form of sexual imprinting seems to facilitate assortative mating and reproductive isolation among closely related cichlid species (Verzijden & ten Cate 2007). Water clarity appears to be important for this mode of speciation, and there is a significant correlation between the number of coexisting haplochromine species and transparency among different East African lakes and among localities within Lake Victoria (Seehausen *et al.* 1997a; Mrosso *et al.* 2004).

Apart from sympatric speciation through disruptive sexual selection, sympatric ecological speciation by disruptive natural selection for resources may have played a role. A potential example concerns the species pair *H. piceatus* Greenwood & Gee, 1969 and *H. coprologus* Niemantsverdriet & Witte, 2010. These species have a similar male colouration, but *H. coprologus*, which used to feed on detritus and phytoplankton, was more deep bodied and had a longer intestine than *H. piceatus* with a diet of zooplankton and insect larvae (De Zeeuw *et al.* 2010). Furthermore, they differed in depth distribution and spawning sites (Goldschmidt *et al.* 1990, 1993; De Zeeuw *et al.* 2010). Sympatric ecological speciation by disruptive natural selection for resources has also been suggested for the cichlid species flock in the Crater Lake Barombi Mbo in Cameroon (Schliewen *et al.* 1994) and for the Lake Tana barbs (Sibbing *et al.* 1998). Finally, allopatric speciation in satellite lakes, that later became connected again to the main lake, probably contributed to species diversity as well (Greenwood 1965, 1974; Kaufman *et al.* 1997). Seehausen (2000) stressed that ‘the evolution of species diversity requires three processes: speciation, ecological radiation and anatomical diversification...’. The functional decoupling of the upper and lower pharyngeal jaws in cichlid fish may have contributed to the third process and may explain the high degree trophic radiation of the haplochromines (Galis & Drucker 1996). However, as Seehausen (2000) suggested, the high degree of phenotypic plasticity in cichlids (e.g. Witte *et al.* 1997), possibly also played a role.

Human induced changes

Fishery in Lake Victoria before the Nile perch boom
In a report on a lake-wide expedition in 1928, Graham (1929) provided an extensive description of the

fishery in Lake Victoria. Perhaps with the exception of scoop nets, netting material was not used in the traditional fishing techniques in Lake Victoria (Graham 1929). Flax gill nets from Europe had been introduced in 1905, but traps, baskets and moving papyrus fences (operated as a kind of seine) were still frequently used in 1928. Even in the 1970s and 1980s traps were still in use in some areas.

From the 1920s till the beginning of the 1950s, the most important food fish of the lake was the tilapiine cichlid *O. esculentus*, but other large fish species such as *O. variabilis*, the lungfish *P. aethiopicus* and the catfishes *C. gariepinus* and *B. docmak* were also fished (Graham 1929; Garrod 1960). In shallow water, women caught the small (< 10 cm total length, TL) cyprinid *R. argentea* by forming a circle, driving the fish to the centre and scooping them from the water with baskets (Graham 1929).

Apart from the widely appreciated *O. esculentus*, the preference for other fish species in Lake Victoria differed locally. For instance, because of its snake-like appearance, the lungfish was disliked by most Wausukuma people living on the south-eastern shores of the lake, but it was highly appreciated by the Wajuluo living around the Nyanza Gulf. The Wahaya and Baganda on the western and northern side of the lake considered *B. docmak* a delicacy. Haplochromine cichlids were popular as food fish among the Wakerewe at Ukerewe Island (Graham 1929; Witte *et al.* 1999).

Fishing down the food web

The introduction of modern fishing gear, like gill nets and beach seines, and the increased demands for fish because of the growing human population and the opening of new markets, due to new roads and railway connections, had a strong impact on the fish catches in the first half of the 20th century (e.g. Graham 1929; Beverton 1959; Fryer & Iles 1972; Balirwa *et al.* 2003; Balirwa 2007). Popular food fish such as *O. esculentus* and the cyprinid *Labeo victorianus* Boulenger, 1901, showed clear signs of over-fishing by the 1940s and 1950s respectively (Cadwalladr 1965; Fryer & Iles 1972; Fryer 1973). The introduction, after the Second World War, of the more catch efficient and long lasting nylon gill nets, and of outboard engines, further increased fishing pressure. The catch per night of native tilapiines in a 50 m-long 127 mm-mesh gill net, decreased from 50–100 fish in 1905 to < 0.5 fish in the same net in 1970 (Kudhonga & Cordone 1974). The minimum mesh size of

127 mm (5 inch) for gill nets was repealed in 1958, which resulted in a short revival and subsequent further dwindling of the catches. The changes in the Lake Victoria fish stocks between 1950 and 1980 conform in a general way to the fishing down model, viz. a dramatic decline in tilapiine catches, followed by a decline in large catfishes and lung fish and an increase in smaller taxa including haplochromine cichlids (Balirwa *et al.* 2003; Welcomme 2005).

Fishery for the small pelagic *R. argentea* using lamps to attract the fish developed in the 1960s and 1970s in Lake Victoria, and was derived from a similar fishery in Lake Tanganyika aiming at clupeids (Okedi 1981). Originally, fish were attracted by lamps attached to rafts that were hauled in slowly to the shore, where the fish were caught with small meshed beach seines. By the end of the 1980s, lift nets and encircling nets, which could be operated offshore, were used to catch the fish that had been attracted by the lamps (Ligtvoet *et al.* 1995).

A lake wide trawl survey in 1969 estimated the standing stock of haplochromine cichlids at 600,000 t (80 % of the demersal fish stock in the lake), and it was suggested that 200,000 t y⁻¹ could be harvested (Kudhonga & Cordone 1974). Ways were sought to exploit this major fish source. Bottom trawling for haplochromines as supply for a fishmeal factory in Mwanza started in the Tanzanian waters in 1976. This factory converted some 10–15 t of haplochromines per day into animal fodder, and signs of local over-fishing of haplochromines in the Mwanza area were reported within a few years (Fig. 2b; Witte & Goudswaard 1985).

Species introductions

To improve the dwindling catches, several fish species were introduced into Lake Victoria in the 1950s (Welcomme 1988). They comprised the Nile perch (*L. niloticus*), Nile tilapia (*O. niloticus*) and the tilapiines *O. leucostictus* (Trewavas, 1933), *Tilapia zillii* (Gervais, 1848) and *T. rendalli* Boulenger, 1896. In the 1980s Nile perch suddenly boomed in Lake Victoria and, concomitantly, the haplochromine cichlids in the sub-littoral and offshore areas vanished almost completely (Fig. 2; Barel *et al.* 1985, 1991; Ogutu-Ohwayo 1990a; Witte *et al.* 1992). These included areas where haplochromines had been fished and already declined, but also areas where there was no fishery on haplochromines. Other species, like the introduced Nile tilapia and especially the native *R. argentea* increased in biomass in the presence of the

Nile perch (Wanink 1999; Goudswaard *et al.* 2002b). The biomass of *R. argentea* increased approximately by a factor of four, but the increase in numbers was about double as high due to a decrease in size of this small cyprinid (Wanink 1999). This strong increase in catch may have been caused by competitive release with the former abundant (zooplanktivorous) haplochromines and a reduction in generation time (Wanink & Witte 2000a). Moreover, in contrast to haplochromines, *R. argentea* were mainly eaten by Nile perch in shallow water (< 12 m deep) but not in the deeper parts of the lake (Katunzi *et al.* 2006). A strong increase was also observed in the biomass of the shrimp *Caridina nilotica*, possibly due to a decreased predation pressure on juvenile shrimps by haplochromines (Goldschmidt *et al.* 1993; Goudswaard *et al.* 2006; Budeba & Cowx 2007b). It took more than 25 years since the first release of Nile perch in Lake Victoria before a dramatic upsurge in the abundance and catch landings of Nile perch was observed. This may have been driven, at least in part, by high survival of very young Nile perch and the food abundance for these fishes. Goudswaard *et al.* (2008), suggested that the abundant haplochromines fed upon eggs and larvae of Nile perch, whenever available. Moreover, the haplochromines were probably competing with juvenile Nile perch for zooplankton and insect larvae. In contrast, a recent study found that the timing and speed of the Nile perch upsurge was not controlled by external triggers and simply grew exponentially (Downing 2012). Nile perch first became noticeably successful in the heavily exploited Nyanza Gulf, Kenya, in 1980. By the early 1970s, over-exploitation of haplochromines was already evident in this area (Marten 1979), which may have facilitated increased survival of juvenile Nile perch. During the subsequent expansion from the Nyanza Gulf towards other areas of the lake, the adult and sub-adult Nile perch fed heavily upon haplochromine cichlids (Hughes 1986; Ogutu-Ohwayo 1990a, b; Mkumbo & Ligtoet 1992) and reduced their numbers to extremely low levels. This process, in some areas like the Mwanza Gulf accompanied by over-fishing of haplochromines, likely enhanced survival of eggs and larvae of Nile perch. After the decline of the haplochromines and the upsurge of the shrimps, juvenile shrimps became an important food item for small (< 10 cm TL) Nile perch (Katunzi *et al.* 2006; Goudswaard *et al.* 2006). Thus, adult Nile perch may have facilitated the survival of their offspring by

eradicating haplochromines that were potential predators and competitors of juvenile Nile perch, but see Downing (2012). However, in some areas of the lake this seems to have been done by heavy fishing on the haplochromines (Goudswaard *et al.* 2008).

Thirty years after its introduction, Nile tilapia had become the most common tilapiine species in Lake Victoria. It replaced the overfished native tilapiines almost completely before the Nile perch came to dominate the ecosystem (Ogutu-Ohwayo 1990a; Goudswaard *et al.* 2002b). The main cause of the final disappearance of the native tilapiine species is presumed to be the competitive dominance of Nile tilapia (Lowe-McConnell 2000, Goudswaard *et al.* 2002b).

In 1989, the South American water hyacinth, *Eichhornia crassipes* (Martius) Solms, 1883 appeared in Lake Victoria. This new intruder quickly established itself (Njuguna 1991). For almost a decade extensive mats of this weed covered large areas along the lake's shores, depriving waters of light and oxygen. To eradicate the weed, locally mechanical removal was applied. Furthermore, South American weevils (*Neochetina eichhorniae* Warner, 1970 and *N. bruchi* Hustache, 1926), were introduced for biological control of the water hyacinth. In 1998 the water hyacinth strongly declined again. However, according to some authors this decline was not only due to the weevils, but also to El Niño events during 1997/1998 that resulted in extensive clouds, which reduced the light conditions and consequently plant growth (Williams *et al.* 2005, 2007). Moreover, shore bound mats were dislodged by raising water levels and driven to open water, where waves helped to destroy them. In the Mwanza Gulf densities of water hyacinth have fluctuated during the past decade, but they have not returned to the peak levels observed in the 1990s (MAKM, JHW and FW pers. obs.).

Environmental degradation and climate change

In the course of the 1980s, frequent blooms of cyanobacteria also became a common feature. They were the result of eutrophication due to the increased human population density, deforestation, and agriculture (Hecky 1993; Mugidde 1993; Scheren *et al.* 2000; Verschuren *et al.* 2002). Losses of phytoplankton through grazing by fish were less than 5% of daily gross and less than 15% of daily net phytoplankton production. As a consequence it is unlikely that the phytoplankton blooms in the second half of the 1980s were due to a top-down effect caused by the strong decline in phyto-

plankton grazing by fish (Witte *et al.* 2012).

Eutrophication and algal blooms caused decreases in water transparency (Mugidde 1993, Seehausen *et al.* 1997a; Witte *et al.* 2005) and in dissolved oxygen levels (Ochumba & Kibaara 1989; Kaufman 1992; Hecky *et al.* 1994; Wanink *et al.* 2001). Sudden upwelling of hypoxic water caused mass fish kills (Ochumba & Kibaara 1989; Ochumba 1990; Kaufman 1992; Kudhongania & Chitamwebwa 1995; Wanink *et al.* 2001; Goudswaard *et al.* 2011). The wetland zone that regulates material transport to the lake has also been under intense pressure from human activities (Balirwa 1995; Kairu 2001). Clearing of papyrus (*Cyperus papyrus* Linnaeus 1753) fringes along the lake shore and conversion of wetlands into agriculture land may have contributed to the decline of lungfish by destroying their breeding habitat (Goudswaard *et al.* 2002a). It has been suggested that water hyacinth mats, which are common since the 1990s, provided a suitable habitat for lungfish and that it played a role in their resurgence in the second half of the 1990s (Bugenyi & Van der Knaap 1997).

Climate change may also have been one of the stressors that affected Lake Victoria (Hecky *et al.* 2010). In the 1990s, the lake was warmer than in the 1960s with a shallower, more stable and more persistent thermocline, which contributed to the deoxygenation of deep water (Hecky 1993; Hecky *et al.* 1994, 2010). Low wind stress that was measured from the mid 1970s to the mid 1990s in Lake Victoria could also have contributed to the longer and more stable anoxic layers (Kolding *et al.* 2008).

LAKE VICTORIA AFTER THE 1980s

Decline of fish diversity

The boom of the introduced Nile perch in the 1980s as well as fishery and habitat deterioration had a strong impact on the haplochromine cichlids and many other fish species (Ogutu-Ohwayo 1990a; Witte *et al.* 1992; Goudswaard & Witte 1997; Goudswaard *et al.* 2002a, b, 2008). It was estimated that some 200 of the endemic haplochromine species may have gone extinct (Witte *et al.* 1992). The highly structured rocky shores and papyrus fringes, where Nile perch densities are low, were less affected by Nile perch than the sub-littoral and offshore waters (Witte *et al.* 1992, 2007a; Seehausen 1996). However, the decrease in water transparency due to eutrophication may have caused hybridization among several haplochromine

species, including those living along rocky shores (Seehausen *et al.* 1997a, 2008; Seehausen 2006). Lake Victoria haplochromines are rather tolerant of low oxygen concentrations (Verheyen *et al.* 1986; Chapman *et al.* 1995; Rutjes *et al.* 2007), therefore the impact of the increased hypoxic conditions due to eutrophication (Hecky *et al.* 1994) may have been less severe than suggested (Witte *et al.* 2005).

Some satellite lakes of lakes Victoria and Kyoga were not invaded by Nile perch or affected by eutrophication. Apart from endemic haplochromine species, these satellite lakes contain some species that are the same as, or similar to, those that vanished from the main lakes; thus providing important refugia for some species and trophic groups (Kaufman & Ochumba 1993; Mwanja *et al.* 2001; Aloo 2003; Mbabazi *et al.* 2004).

Nile perch predation, competition with introduced species, habitat deterioration and fishing pressure also contributed to declines in other native species including catfishes [*B. docmak*, *Xenoclaris eupogon* (Norman, 1928), *Synodontis victoriae* Boulenger, 1906], the lungfish *Protopterus aethiopicus*, the mormyrid *Mormyrus kannume* Forsskål, 1775, the cyprinid *Barbus altianalis radcliffi* Boulenger, 1903 and the tilapiines *O. esculentus* and *O. variabilis* (Table 2; Goudswaard 1988; Ogutu-Ohwayo 1990a; Goudswaard & Witte 1997; Goudswaard *et al.* 2002a, b). However, the impacts of the above described human induced threats were not the same for all fish species. In several cases a threat to one species did have a positive effect on another species; e.g. the decline of haplochromines by Nile perch predation had a positive effect on the population of *R. argentea* (Table 2).

Resurgence of some haplochromine species

In the course of the 1990s, after a decline of Nile perch in Lake Victoria due to intensive fishing, a slow resurgence of some haplochromine species was observed in the sublittoral waters (Witte *et al.* 2000, 2007a, b; Balirwa *et al.* 2003; Getabu *et al.* 2003). Similar observations were made in Lake Nabugabo, a shallow satellite lake of Lake Victoria (Ogutu-Ohwayo 1993; Chapman *et al.* 2003).

The resurgence in Lake Victoria, mainly concerned zooplanktivorous and detritivorous haplochromines, but of each group only about 30% of the species recovered, and initially the ratio in biomass of detritivores and zooplanktivores was reversed (Witte *et al.* 2007a, b). Before the 1980s detritivores made up about 50% of the haplochromine biomass in the sublittoral waters

Table 2. Human induced changes and their impacts on various fish stocks (neg = negative; pos = positive).

Change	impact	on:
Increased fishery	neg	Most fish species (esp. native tilapiines + large cyprinids) and finally on Nile perch
Increased Nile perch	neg	Most fish species (esp. haplochromines), but not on <i>R. argentea</i> and Nile tilapia
Increased Nile tilapia	neg	Native tilapiines
Habitat deterioration	neg	Lungfish + <i>C. gariepinus</i> ?
Increased eutrophication	neg	Especially haplochromines (hybridization)
Increased water hyacinth	pos	Lungfish and <i>C. gariepinus</i> and possibly some other fish species that could cope with low oxygen levels and limited light conditions
Decreased haplochromines	pos	Juvenile Nile perch, shrimps and <i>R. argentea</i>

Table 3. Preliminary data on ecological and morphological changes in resurging detritivorous (Detr), zooplanktivorous (Zoo) and oral shelling molluscivorous (Or sh) haplochromine species. Numbers represent the number of species in which the changes were observed. Note that absence of changes may imply that no changes were observed or that the trait has not yet been studied.

Trophic group (number of species)	Detr (2)	Zoo (3)	Or sh (1)	Sources
Trait				
Habitat change	2	3	1	1, 2, 3
Increased fecundity	-	3	-	4, 5
Diet	2	3	1	1, 6, 7, 8, 9
Intestine length	2	-	-	8
Head volume	-	3	-	10, 11
Body shape	1	3	1	12
Eye size	-	3	1	10, 12, 13
Retina	-	2	-	13, 14
Muscles feeding app	-	1	-	10
Dentition premaxilla	-	2	1	9
Gill raker number	-	1	-	11
Gill surface area	-	2	1	10, 11

Sources = ¹van Oijen & Witte 1996; ²Seehausen *et al.* 1997b; ³Kishe-Machumu 2012; ⁴Wanink 1991; ⁵JHW unpublished; ⁶Wanink 1998; ⁷Katunzi *et al.* 2003; ⁸Kishe-Machumu *et al.* 2008; ⁹Van Rijssel *et al.* submitted; ¹⁰Witte *et al.* 2008; ¹¹JCVR unpublished; ¹²Van Rijssel & Witte 2013; ¹³Van der Meer *et al.* 2012; ¹⁴Witte *et al.* 2005.

of the Mwanza Gulf and zooplanktivores about 25% (Fig. 3b; Goldschmidt *et al.* 1993), whereas by 2005 detritivores constituted only 26% and zooplanktivores more than 70% (Witte *et al.* 2007a). In 2008 and in February - April 2011, detritivores were the dominant group again (Kishe-Machumu 2012; MAKM, JCVR and FW pers. obs.). However, the majority of the species did not recover (Witte *et al.* 2007a). In spite of frequent sampling in the Mwanza Gulf in the period between 1987 and 2011, many of the highly specialized trophic types like scale eaters, parasite eaters and prawn eaters have not been caught, whereas piscivores and paedophages are extremely rare now, both with respect to numbers of individuals and species. Similar results were found by Mizoiri *et al.* (2008) who sampled the Mwanza Gulf and the Speke Gulf at many localities in 2004, 2005 and 2006.

Nile perch longer than 20 cm total length, which since the disappearance of the haplochromine cichlids mainly fed on shrimps, its own juveniles and *R. argentea* (Hughes 1986; Ogutu-Ohwayo 1990b; Mkumbo & Ligtoet 1992; Katunzi *et al.* 2006), switched again to haplochromines after their re-emergence (Budeba & Cowx 2007a; Kishe-Machumu *et al.* 2011).

Responses to environmental changes

Apparent responses to the environmental changes were observed in several fish species in the Mwanza Gulf. Some haplochromine species extended their use of habitat (Table 3). Most striking were the zooplanktivorous *Haplochromis (?) tanaos* van Oijen & Witte, 1996 and the snail shelling *Haplochromis*

(*Paralabidochromis plagiodon* Regan & Trewavas, 1928, which formerly were restricted to the shallow (< 6 m) sand stations in Butimba Bay. Since the resurgence of the species in the 1990s, both occur predominantly over mud bottoms up to 11 m depth (Seehausen *et al.* 1997b; Kishe-Machumu 2012; MAKM, JHW, JCVR and FW unpublished data). In contrast the zooplanktivore *Haplochromis (Yssichromis) pyrrocephalus* Witte & Witte-Maas, 1987 now also occurs in shallower areas than in the past. Reproductive strategies changed in the Nile tilapia (Ojuok *et al.* 2007) and the cyprinid *R. argentea* (Wanink & Witte 2000a; Manyala & Ojuok 2007); both have shown a decrease in their size at maturity. In the zooplanktivorous haplochromines, *Haplochromis (Yssichromis) laparogramma* Greenwood & Gee, 1969, *H. pyrrocephalus* and *H. tanaos*, an increase of both absolute and relative fecundity have been observed (Wanink 1991; Wanink & Witte 2000a; JHW unpublished data).

Dietary shifts were observed in zooplanktivorous and detritivorous/phytoplanktivorous haplochromines (van Oijen & Witte 1996; Katunzi *et al.* 2003; Kishe-Machumu *et al.* 2008; van Rijssel *et al.* submitted) as well as in the oral shelling haplochromine *Platytaeniodus degeni* Boulenger, 1906 (van Rijssel *et al.* submitted). In all these cases the amount of macroinvertebrates in the diets increased strongly. Similar changes in diet were found in other fish taxa (Table 4). These changes were also reflected in comparisons of stable isotopes of detritivorous and zooplanktivorous haplochromines between the pre- and post-Nile perch

Table 4. Dominant food items in diets of different fish taxa from Lake Victoria before and after the ecological changes in the 1980s.

Taxon	before 1980s	1990s -2006
Zooplanktivorous hapl. (3 sp.) ^{1,2,3}	zooplankton	Macroinvertebrates (+zoopl)
Detritivorous hapl. (> 3 sp.) ⁴	detritus/phytoplankton	macroinvertebrates
<i>Platytaeniodus degeni</i> ³	detritus (+ molluscs)	macroinvertebr (+ molluscs)
<i>Bagrus docmak</i> ⁵	haplochromines	insects, <i>R. argentea</i>
<i>Schilbe intermedius</i> (Linnaeus, 1758) ⁵	haplochromines	insects
<i>Rastrineobola argentea</i> ^{6,7}	zooplankton	macroinvertebr, fish
<i>Brycinus sadleri</i> (Boulenger, 1906) ⁸	plants, insects	macroinvertebrates
Nile tilapia ^{7,9,10,11}	detritus/phytoplankton	macroinvertebrates

¹van Oijen & Witte 1996; ²Katunzi *et al.* 2003; ³Van Rijssel *et al.* submitted; ⁴Kishe-Machumu *et al.* 2008; ⁵Olowo & Chapman 1999; ⁶Wanink 1998, ⁷Budeba & Cowx 2007a; ⁸Wanink & Joordens 2007; ⁹Gophen *et al.* 1993; ¹⁰Bwanika *et al.* 2006; ¹¹Njiru *et al.* 2007.

era (Kishe-Machumu 2012). In the detritivorous/phytoplanktivorous haplochromines the shift in diet was accompanied by a decrease of 30% in relative intestine length (Kishe-Machumu *et al.* 2008). As discussed by Kishe-Machumu *et al.* (2008) potential factors for these diet shifts could be: (a) the increased availability of profitable food items; (b) the loss of competitors, and (c) the increased water turbidity after the environmental changes. In the last case, it is supposed that the fish that grew up under low light conditions changed their retina in such a way that they increased their light sensitivity at the cost of their resolution (e.g. Van der Meer 1993; Van der Meer *et al.* 2012).

Some resurgent zooplanktivorous species showed body shape changes as a response to the environmental changes while other zooplanktivores, which are thought to be extinct or poorly recovered, showed changes in the opposite direction (Van Rijssel & Witte 2013). One of the resurgent species is the zooplanktivorous *H. pyrrhocephalus* which is currently the most common haplochromine cichlid in the Mwanza Gulf, and its morphology has been studied extensively. A comparison of specimens collected in the 1970s (pre-Nile perch population) and those collected in the 1990s (modern population) revealed that head length and head volume (for *H. pyrrhocephalus*) decreased in three different haplochromines (Witte *et al.* 2008; Van Rijssel & Witte 2013). These size decreases match biomechanical predictions for increased swimming speed in presence of predators (Langerhans *et al.* 2004, Chapman *et al.* 2008). The gill surface area in resurgent *H. pyrrhocephalus* increased by 64%, which is an apparent adaptation to the increased hypoxic conditions. The gill rakers decreased in length and the cheek depth and the *musculus levator posterior*, responsible for biting force of the pharyngeal jaws, increased in size (Witte *et al.* 2008). These changes may reflect adaptive responses to the larger and tougher prey types in the diet of modern *H. pyrrhocephalus* (Katunzi *et al.* 2003). Reductions in eye size and in the size of the *musculus sternohyoideus*, and reallocation of space among compartments of the head seem to have permitted accommodation of larger gills in a relatively smaller head (Witte *et al.* 2008).

A reduction in eye size was also observed in *H. tanaos*. However, it was also observed that while the density of the blue sensitive single cones were reduced, the size of the red and green cones in the retina had increased (Witte *et al.* 2005; Van der Meer *et al.* 2012). In eutrophied water with high algae concentrations,

blue light is filtered out faster than red and green light. So, blue sensitive cones may be of reduced relevance in the current visual habitat of *H. tanaos*. In spite of its reduced eye size, light sensitivity was probably improved by the increased size of the double cones, but at the cost of the resolving power. However, as it currently feeds on larger prey, the loss of resolution may not have much impact on feeding performance of *H. tanaos*. Finally, preliminary studies suggest changes in oral dentition in several of the recovering species, which also may be related to the change in diet (Van Rijssel *et al.* submitted).

Though less striking than in the haplochromine cichlids, morphological changes were also observed in the cyprinid *R. argentea*; the number of gill filaments increased, whereas the number of gill rakers decreased, possibly in response to the lower oxygen concentrations and larger prey, respectively (Wanink & Witte 2000b).

The rapid morphological changes described above may reflect environmentally induced plasticity, heritable response to natural selection, genetic introgression through hybridisation or, most likely, a combination of several of these factors. Recent studies of contemporary evolution in natural populations, especially in response to environmental changes caused by human activity, yielded estimates of potential rates of evolution many orders of magnitude greater than rates inferred from the fossil record (e.g. Carrol *et al.* 2007).

Fishery in Lake Victoria after the Nile perch boom

By the end of the 1980s only three fish species were common in sub-littoral and offshore waters of Lake Victoria. These were the small indigenous cyprinid *R. argentea* and the introduced Nile perch and Nile tilapia (Fig. 2a; Ogutu-Ohwayo 1990a; Wanink 1999; Goudswaard *et al.* 2002b). Together, they dominated the fish landings by more than 80% (Fig. 2a; Reynolds *et al.* 1995).

Although biodiversity decreased strongly and water quality deteriorated, fish production in Lake Victoria flourished after the Nile perch boom. In the 1960s, the total landings for the lake were approximately 100,000 t y⁻¹. In the late 1980s and early 1990s, just after the Nile perch boom, the fisheries produced over 500,000 t of fish annually (Balirwa 2007). Concomitantly, bottom trawl catches revealed that the standing stock of demersal fish had decreased about five times (Fig. 2 b; Okaroon 1994; Witte *et al.* 1999; Balirwa 2007). This indicates that the dramatic increase of the

total fish landings reflected an increase in fishing effort, which was indeed observed during the past decades (Ogutu-Ohwayo 2004; Matsuishi *et al.* 2006; Balirwa 2007). The number of fishers and fishing boats tripled between 1990 and 2007 (Fig. 4; Ogutu-Ohwayo 2004; Matsuishi *et al.* 2006; Mkumbo *et al.* 2007).

Since the 1980s, the total annual landings in the lake increased, but by the mid 1990s the contribution of Nile perch showed some decline, whereas landings of *R. argentea* and Nile tilapia increased (Fig. 4; Matsuishi *et al.* 2006). Just after the boom, Nile perch contributed more than 70% to the fish landings (Figs 2, 4; Van der Knaap *et al.* 2002), but between 1990 and 2000 the catch per unit effort of Nile perch dropped from about 80 to 45 kg per boat per day in the Kenyan waters, where adequate data had been collected (Matsuishi *et al.* 2006). By 2000 the total annual landings amounted to 657,000 t, 40% of which was made up by Nile perch, 41% by *R. argentea* and 8% by Nile tilapia (calculated from Table 1 in Matsuishi *et al.* 2006). The landings of haplochromine cichlids had increased from virtually zero at the end of the 1980s to 17,000 t y⁻¹ in the Tanzanian waters, whereas in Kenyan waters the catches were only 300 t y⁻¹ (Matsuishi *et al.* 2006).

In the period 2005-2007, the annual landings were even estimated at 1 million t and the contribution of Nile perch was about 26%, while that of *R. argentea* had increased to about 53% (Fig. 4, LVFO, CAS Report 2006). Apparently, the species composition in the fish landings has changed toward lower trophic level species (viz. *R. argentea* and Nile tilapia, Matsuishi *et al.* 2006). Hydroacoustic surveys between 1999 and 2008 suggested that over the studied period the overall fish biomass in Lake Victoria remained more or less constant, but the biomass of Nile perch decreased, whereas that of *R. argentea* increased (Fig. 5; Getabu *et al.* 2003; Mkumbo *et al.* 2005; LVFO Hydroacoustic Survey Report 2007; LVFO, IFMP 2, 2008; Kayanda *et al.* 2011). The foregoing seems to represent a second fishing down episode in Lake Victoria (Balirwa *et al.* 2003).

Originally, the fishermen did not like Nile perch because they had problems with handling, processing and marketing the fish; the larger and relatively fat perch could not easily be dried or transported. However, in the years after the upsurge, people rapidly adjusted the processing and transport techniques. The larger fishes were chopped into pieces and subsequently fried in the fat removed from the intestines

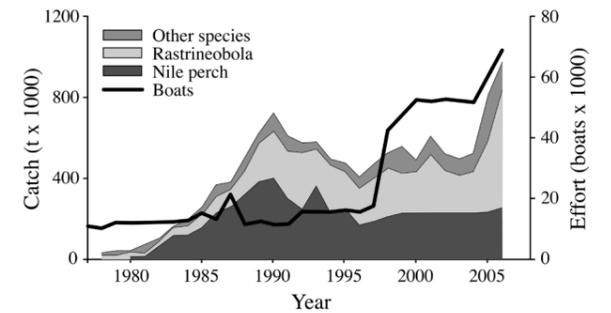


Fig. 4. Trends in total annual fish landings and total fishing effort in Lake Victoria during the period 1975 – 2005. Nile tilapia is included in 'other species'. Note that the increase in effort was mainly directed at Nile perch (effort data from LVFO Frame Survey Report, 2006; Catch data from LVFO IFMP 2, 2008; Figure from Witte *et al.* 2009b).

(Ligtvoet 1989; Ligtvoet *et al.* 1995). The smaller ones were dried in the sun or smoked. For frying and smoking firewood was needed, thus the Nile perch boom strongly exacerbated the ongoing deforestation along the lake shore. In the 1990s filleting factories arose for export of Nile perch fillets to Europe and Asia (Ntiba *et al.* 2001). The total capacity of these factories is several hundred tons per day, and they became the main buyers of Nile perch. Many of these fish processing plants now operate below their installed capacity. Balirwa (2003) reports that in Uganda, 15 factories with a total installed capacity of 420 t per day, are actually processing 185 t per day. Currently, about 1.2 million people are directly or indirectly dependent for their livelihood on the fishery in Lake Victoria (Matsuishi *et al.* 2006). In 2003 the estimated annual catch was worth at least US\$ 540 million at the fish landings, whereas a further US\$ 240 million was

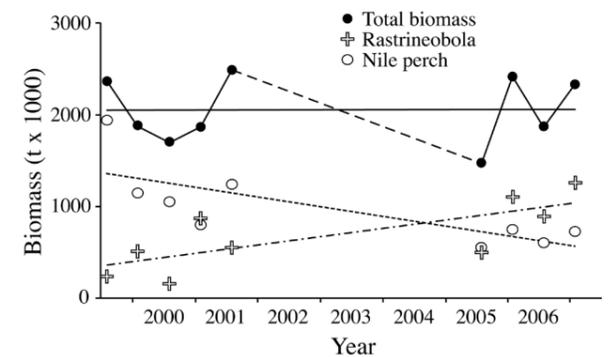


Fig. 5. Estimated fish biomass in Lake Victoria based on acoustic surveys in the periods 1999-2001 and 2005-2007. Note that the equipment and analytical protocols differed between the periods 1999–2001 and the period 2005–2007 (after LVFO, Hydroacoustic survey Reports 2006 & 2007; Figure from Witte *et al.* 2009b).

earned in fish exports (Balirwa 2007).

Several observations, e.g. the decline in annual landings and the decline in size at first maturity, suggest that Nile perch is intensively fished, which may result in overexploitation. Consequently, it has been suggested that, under the scenario of increased fishing effort, the Nile perch fishery is unsustainable (Pitcher & Bundy 1995; Mkumbo 2002; Matsuishi *et al.* 2006; Mkumbo *et al.* 2007; Kayanda *et al.* 2011). However, according to Kolding *et al.* (2008) not over-fishing, but the ongoing eutrophication is the main threat to the Nile perch fishery. Based on Chl α measurements by Silsbe *et al.* (2006) and annual Nile perch catches, Kolding *et al.* (2008) suggest that the top of the productivity curve for Nile perch as a function for eutrophication has been reached.

In the past, the management measures governing Lake Victoria resources were different in each country (Ntiba *et al.* 2001). Through the Lake Victoria Fisheries Organization (LVFO) that was formed in 1994 and support from the EU to implement a Management Plan, attempts to harmonize policies and regulations and also to develop standard operational procedures are continuing. Lake-wide management regulations are established, and a co-management approach has been adopted. About 1060 Beach Management Units (BMUs) have been established around Lake Victoria to take an active role in management of the resources at beach level (LVFO Website www.lvfo.org). The harmonized rules include: banning of beach seines, bottom trawls and cast nets, and of gill nets below 13 cm (5 inches) mesh size; as well as implementation of a slot size of 50 to 85 cm total length for Nile perch (Kizza *et al.* 2005).

CONCLUSION

Dramatic changes occurred in the ecosystem and fish fauna of Lake Victoria during the past century as a result of human activities in and around the lake. The Nile perch boom altered the biomass distribution over trophic levels from a pyramid shape at the end of the 1970s to a top-heavy shape at the end of the 1980s, while by 2005, the pyramid shape was regained again (Downing *et al.* 2012). Nevertheless, many species, especially among the haplochromine cichlids, declined or even disappeared. Still there is hope for the future as a resurgence of some haplochromine species has been observed. Balirwa *et al.* (2003) suggested that conservation of biodiversity and fishery sustainability may not be in conflict in the manage-

ment of Lake Victoria. A modelling study suggested that Nile perch prefer and grow fastest on a haplochromine prey base (Kaufman & Schwarz 2002). If the model is realistic, it would suggest that it is worth thinking of management strategies that allow sufficient fishing on Nile perch to ensure an abundance of their haplochromine prey, but not so much pressure as to threaten the Nile perch stock itself (Balirwa *et al.* 2003). However, to allow maintenance and restoration of haplochromine diversity and of other fish species, the urgent measures must include serious attempts to reverse the eutrophication of Lake Victoria (Seehausen *et al.* 1997a; Balirwa *et al.* 2003; Witte *et al.* 2005; Kolding *et al.* 2008).

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